

POLLEN AND POLLINATION IN THE EUPOMATIACEAE.

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(Plate ii; twenty-six Text-figures.)

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Synopsis.

The formation of the microspores in *Eupomatia laurina* is described and illustrated. Standard descriptions and illustrations of the pollen grains of both *E. laurina* and *E. bennettii* are given. Pollination in *E. bennettii* is similar to that in *E. laurina*. Comparisons are made with other ranalian plants.

INTRODUCTION.

More information is needed as a basis for understanding the structure and relationships of the woody ranalian plants. As a beginning of a series of papers on the Eupomatiaceae, the geographical distribution of the family has been described (Hotchkiss, 1955). It is hoped that the present paper will be followed by additional information on this interesting family as studies are completed on various anatomical and morphological details. Materials were collected in New South Wales and Queensland as indicated in the text.

MICROSPOROGENESIS.

The long, narrow, sunken sporangia are closely filled with microspore mother cells within cell walls which vary from an angular, isodiametric to a rather elongate form which persists through the tetrad stage (Text-figs. 1-22). During meiosis the cell wall thickens and becomes gelatinous in appearance. In *Eupomatia laurina*, meiosis in the microspore mother cells is normal and ten bivalents can be seen at metaphase I. These usually separate in a synchronous anaphase (Text-figs. 1-2). Infrequently, at anaphase I, however, there appears to be early separation of one bivalent, as shown in Text-figures 3-5; there also may be a tardy separation of one or more bivalents (Text-figs. 6-8).

After division I, a cleavage furrow begins to form as in *Magnolia* (Farr, 1918) but stops with the formation of an internal ridge filled with wall material at the beginning of division II (Text-figs. 9-10). At the end of the second division, the first furrow continues its growth and at the same time additional furrows appear. Then, simultaneously, all the furrows divide the mother cell into four compartments containing the microspores (Text-figs. 11-16). At interkinesis there is a conspicuous spindle fibre apparatus remaining between the two dyad cells (Text-figs. 9-10). At the completion of meiosis II, spindle fibres are conspicuous between the nuclei of the tetrad and remain so until the cytoplasmic connections between the microspores are finally cut off by the advancing furrows (Text-figs. 11-16). From the more isodiametric young tetrads with 4-6 spindles there develop the commoner tetrahedral, isobilateral, rhombic and decussate tetrads enclosed in nearly spherical mother cell walls; from the linear, young tetrads with spindle connections between only the closely adjacent nuclei, there develop the rarer linear and T-shaped tetrads enclosed in elongate mother cell walls (Text-figs. 17-22).

POLLEN.

The pollen grains of *Eupomatia laurina* have been figured by Hamilton (1897), figured and described by Erdtman (1952). The pollen grains of both species of

Eupomatia are here figured and described (following the system of Erdtman) with additional details as follows:

Eupomatia laurina R. Br. (Text-fig. 23). Bulli Pass, New South Wales. Grains nearly spherical, spheroidal prolate; zonisulculate with a distinct groove on either side of the equatorial zone, rarely 3-sulculate; exine finely granular in the sulculus-zone;



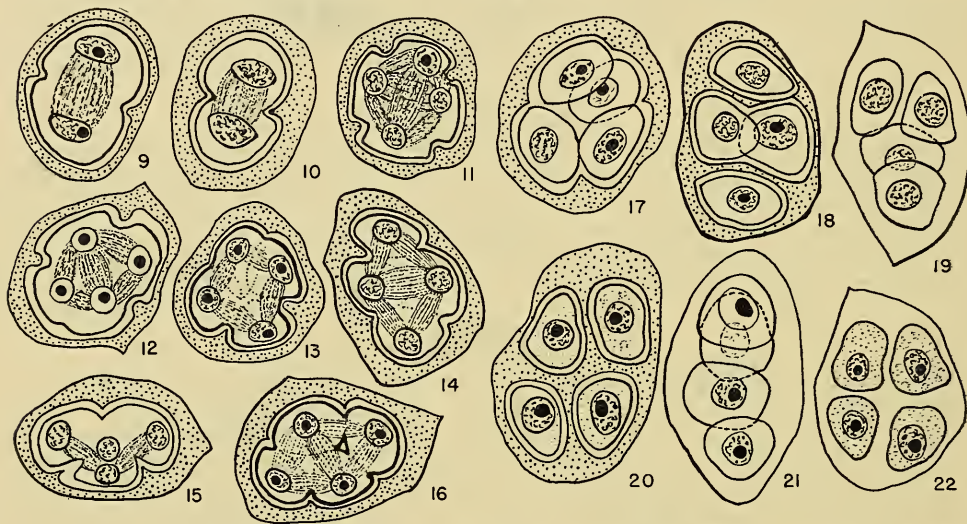
Text-figs. 1-8.—*Eupomatia laurina*, meiosis. 1, Metaphase I; 2, Anaphase I; 3-5, Metaphase I with early separation of a bivalent; 6-8, Anaphase I with tardy separation of bivalents. $\times 862$.

polar axis slightly longer, from 44 to 50 μ , the equatorial diameter shorter, from 43 to 48 μ .

Eupomatia bennettii F. Muell. (Text-fig. 25). Bellingen, New South Wales. Grains: nearly spherical, more or less rectangular in section; at first nearly isopolar, later one pole protruding; zonisulculate; exine finely granular in the sulculus-zone, granules

finer than in *E. laurina*; polar axis slightly shorter, from 35 to 40 μ , the equatorial diameter longer, from 37 to 44 μ .

In *E. laurina* an occasional tetrad remains coherent and thus indicates the polar-equatorial relationship. The young pollen grain bulges in the equatorial zone because of the folding of the thickened wall in a two-pleated manner. This results in the formation of a broad equatorial ridge bounded on either side by furrows which extend completely around the pollen grain in *E. laurina* (zonisulcate—Erdtman, 1952) and nearly around in *E. bennettii*. As the grain is expanded the flexible equatorial zone straightens out although the grooves impressed on the protoplast remain; when the grain is dried the walls are refolded and contract again (Text-fig. 26). Occasional pollen grains may be seen germinating within the anther. In *E. laurina* the pollen tube emerges from one of the grooves (Text-fig. 24). What appears to be a beginning pollen tube can often be seen growing from the apex of the pollen grain of *E. bennettii* (thus changing its isopolar shape) in Text-fig. 26.



Text-figs. 9-16.—*Eupomatia laurina*, developing microspores. 9-10, Arrested cleavage furrows at interkinesis; 11-16, Spindles and cleavage furrows developing after meiosis II. The lobing of the future microspores can be seen before the furrowing is completed but no cell plates are present. $\times 937$.

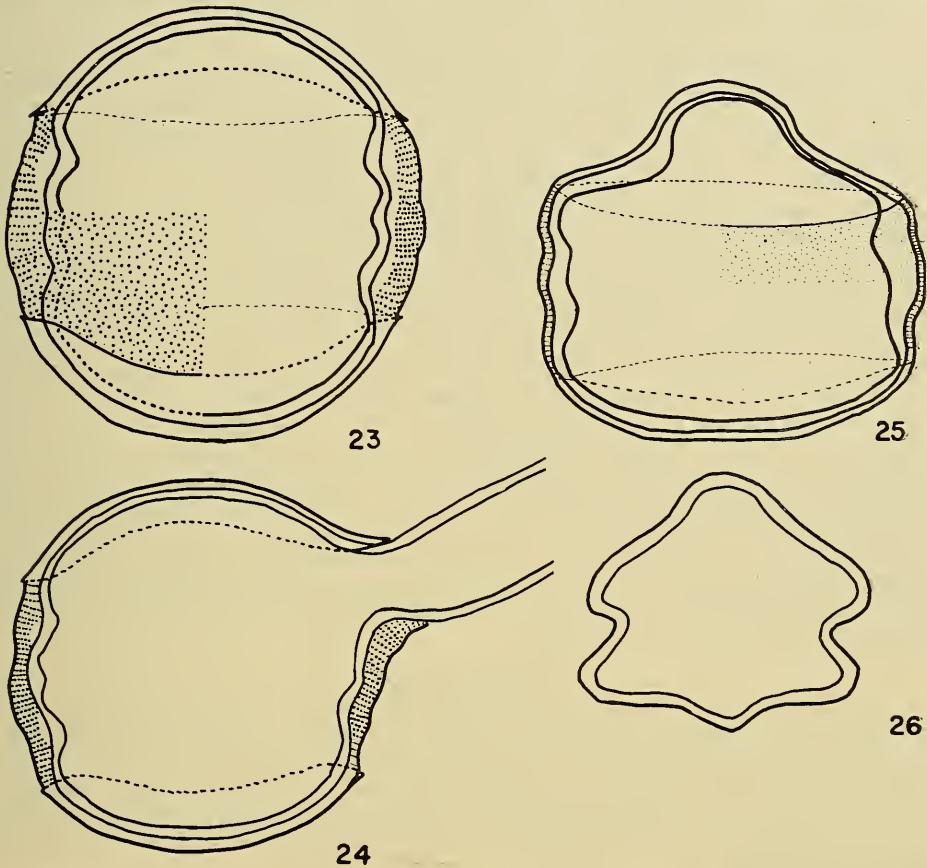
Text-figs. 17-22.—*Eupomatia laurina*. Tetrads after cleavage showing some arrangements of microspores. $\times 937$.

POLLINATION.

Robert Brown (1814) discussed the unusual pollination mechanism in *Eupomatia laurina* "by certain minute insects eating the petal-like filaments (staminodia), while the antheriferous stamina . . . remain untouched". Bennett (1860) reported that Harvey in 1834 had found a small brown *Curculio* on *E. laurina* in the Illawarra district of New South Wales. Hamilton (1897) confirmed the presence of beetles in the flower of *E. laurina* and described in detail the behaviour of this insect, *Elleschodes hamiltoni* T. Blackburn. To this account there can be added that the overarching, inner, rather fleshy staminodes are equipped with succulent glands composed of delicate secretory-like cells. Although the glands may be the first objective of the feeding beetles, a large portion of the staminode is often consumed. No nectar has been observed. From flowers placed in the laboratory, beetles emerge in the early evening darkness and fly about. During the day, in the laboratory or the field, they show little tendency to leave the flowers or to fly at all. Besides the Illawarra district and Bulli Pass, beetles of this species have been collected from the upper Williams River valley (Messmer and Musgrave, 1944), and south-east Queensland.

From flowering plants of *E. bennettii* at Bellingen, New South Wales, collections of similar beetles were made in September, 1954. These were kindly identified by

Mr. A. Musgrave, of the Australian Museum, Sydney, as *Elleschodes* sp. In this connection it may be noted that the flowering time of *E. bennettii* is several months removed from that of *E. laurina*, and that the latter species flowers and fruits heavily every other year and apparently not at all in the intervening years.



Text-figs. 23-24.—*Eupomatia laurina*. 23, Mature pollens grain; 24, Germination of pollen grain from one of the grooves. $\times 1150$.

Text-figs. 25-26.—*Eupomatia bennettii*. 25, Mature pollen grain; 26, Outline of partly dried pollen grain. $\times 1150$.

DISCUSSION.

The irregularities in anaphase I seem to have little effect on the subsequent maturation of the tetrads which almost invariably are filled with four microspores of equal size. Farr (1916) reported that the primary spindle persists in *Nicotiana* and that four new and identical spindles were formed after the second division. However, in *Magnolia*, Farr (1918) states that the primary spindle completely disappears as meiosis II begins and that in telophase II a large number of fibres again appear. Whether or not in *Eupomatia* the fibres of the primary spindle disappear as in *Magnolia* remains undetermined. In *Nicotiana* there is neither a cell-plate nor a furrow formed between meiosis I and II; in *Magnolia* both these structures are initiated, although neither is completed before meiosis II (Farr, 1916, 1918). *Eupomatia* resembles *Magnolia* in possessing the arrested cleavage furrow but it lacks the cell-plate vestige. In *Eupomatia* the persistent shape of the microspore mother cell wall is related to the arrangement of the tetrad contained therein. Farr (1916) states that it is quite probable that "the restraining tension of the wall has very little to do with initiating the tetrahedral arrangement, though it may play a large part in the

maintenance of such orientation". The tetrads of *E. laurina* include the range of forms (with intergradations) as shown by Maheshwari (1950) for the angiosperms. In the Degeneriaceae, simultaneous divisions of the microspore mother cells result in tetragonal tetrads (Swamy, 1949), in the Anonaceae the divisions are successive in *Asimina triloba* (Locke, 1936), and successive or nearly so in *Anona* (Juliano, 1935).

Erdtman (1952) points out that the pollen grains of *Eupomatia* are similar to the 2- and 3-sulcate type found in the Atherospermoideae, and the sulcate pollen of the Calycanthaceae. Possession of this type of pollen at once establishes the position of the Eupomatiaceae in the Ranales (*sensu lato*) and, with some other features, associates this family with those woody families generally considered the least specialized in the order (Bailey and Nast, 1943; Bailey and Swamy, 1949; Canright, 1953; Swamy and Bailey, 1949; Wodehouse, 1935). Sulcate pollen is derived from the monocolpate (one-furrowed—Wodehouse, 1935) pollen and distinguished from the tricolpate pollen found in the majority of dicotyledonous plants.

Entomophily and, more specifically, pollination by beetles, has been considered by various workers to possess considerable phylogenetic significance. The flowers of *Eupomatia* (Plate ii) correspond to "the simple level with a haplomorphic arrangement of petals" (Leppik, 1957). The strong, fruity, penetrating odour, and the generally creamy white colour also suggest this classification. The nutritive tissues which are confined to the tips of the inner floral appendages in *Calycanthus* (Grant, 1950) are scattered over the margins and inner surfaces of the over-arching inner stamnodes in *Eupomatia*. Diels, in a paper on Käferblumen (1916), compared beetle pollination in *Eupomatia* with that in *Calycanthus*, other ranalian plants, and in *Encephalartos*. He suggested that beetles may have been one of the earliest existent orders of insects to be anthophilous. The same views have been expressed by Grant (1950), whose investigations on the pollination mechanism in *Calycanthus occidentalis* reveal a striking similarity between that plant and *Eupomatia*. Grant sums up the evidence from living plants and fossils for the hypothesis that beetle pollination was the original condition in flowering plants.

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EXPLANATION OF PLATE II.

Eupomatia bennettii F. Muell.—The solitary, terminal flower. A few of the thin, narrow, petal-like, outer staminodia are seen reflexed at the right. Above these the staminodia are longer, broad and fleshy. The arching, very fleshy, inner staminodia bear the glands of nutritive tissue. The fertile stamens are invisible beneath the outer staminodia. Plant collected at Bellingen, New South Wales. $\times 1.25$. (Photograph by Woodward-Smith.)